NeoBiota 82: 23–56 (2023)
doi: 10.3897/neobiota.82.96282
https://neobiota.pensoft.net

RESEARCH ARTICLE

A peer-reviewed open-access journal
NeoBiota
Advancing research on alien species and biological invasions

The TOP-100 most dangerous invasive alien species in Northern Eurasia: invasion trends and species distribution modelling

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Academic editor: Helen Sofaer | Received 13 October 2022 | Accepted 17 January 2023 | Published 2 February 2023

Citation: Petrosyan V, Osipov F, Feniova I, Dergunova N, Warshavsky A, Khlyap L, Dzialowski A (2023) The TOP-100 most dangerous invasive alien species in Northern Eurasia: invasion trends and species distribution modelling. NeoBiota 82: 23–56. https://doi.org/10.3897/neobiota.82.96282

Abstract

Northern Eurasia is extensive and includes terrestrial and aquatic ecosystems that cover several natural zones and access to the seas of three oceans. As a result, it has been invaded by numerous invasive alien species (IAS) over large temporal and spatial scales. The purpose of this research was to assess invasion trends and construct species distribution models for the Russian TOP-100 most dangerous IAS. Environmentally suitable regions for IAS were established based on alien species attribute databases, datasets of 169,709 species occurrence records (SOR) and raster layers of environmental variables using species distribution modelling (MaxEnt). The objectives of this research were to (1) create databases of SOR for the TOP-100 IAS in Russia; 2) determine pathways, residence time, donor regions and trends of invasions; (3) determine the main types of spatial distributions of invasive species and their relation to residence time; and (4) distinguish regions with the highest richness of IAS that have a strong impact on the terrestrial and aquatic ecosystems of Russia. We found that although species invasions date back over 400 years, the number of naturalized IAS has increased non-linearly over the past 76 years. The TOP-100 list is mainly represented by unintentionally introduced species (62%) which are characterized by different introduction pathways. Species occurrence records revealed that 56 IAS are distributed locally, 26 are distributed regionally and 18 are widespread in Russia. Species with local, regional or widespread distributions were characterized by residence times of 55, 126 or 190 years, respectively. We found that IAS with local distribution can expand their range into suitable regions more extensively (expected increase by 32%) than widespread species (expected increase by only 7%). The procedure of identifying hot/cold spots locations based on SOR allowed us to identify the Russian regions with the highest richness of IAS. Our results and the integrated database that we created provide a framework for studying IAS over large temporal and spatial scales that can be used in the development of management plans for dangerous IAS.

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Keywords
animals, biological invasions, donor regions, hot spots, microorganisms, plants, SDM, species occurrence records

Introduction

Globalization, changes in climate and land use, and increased traffic flows have accelerated the rates of introduction of invasive alien species (IAS) to unprecedented levels and allowed them to overcome fundamental biogeographic barriers (Richardson 2011; Seebens et al. 2018). This increase in the spread of IAS is one of the principal features of the Anthropocene Era (Crutzen 2002; Lewis and Maslin 2015). Many countries around the world develop and implement science-based biosafety strategies in response to current and potential invasions of alien species (Wittenberg and Cock 2001; Clout and Williams 2009) to conserve biodiversity (Convention on Biological Diversity 2010) and promote the sustainable development of ecosystems (Transforming our world 2015). One of the challenges for minimizing the risk of invasions and potential losses in the environmental, socio-economic and medical spheres at local, regional and global levels is to identify priority alien species and locations to incorporate into ecological management (Wittenberg and Cock 2001; Stohlgren and Jarnevich 2009). As part of such activity, the 100 most dangerous IAS for the World (TOP-100 World) were identified (Weijden et al. 2007). Within the framework of the SEBI 2010 project (Streamlining European Biodiversity Indicators 2010) (Biała et al. 2012), the European Environment Agency compiled a list of the 100 most aggressive alien species for Europe (TOP-100 Europe) that threaten biodiversity (European Environment Agency 2007; DAISIE 2009; Nentwig et al. 2018). In addition, there are other national and regional lists of the most dangerous IAS. These lists have been prepared for European countries including Czech Republic, France, Italy, and Spain; and regions including the Mediterranean, Northern Europe and Baltic regions (DAISIE 2009). In particular, the international network NOBANIS (North European and Baltic Network on Invasive Alien Species, http://www.nobanis.org) includes the most dangerous IAS (TOP-82 NOBANIS) of the participant countries of this system (Austria, Belgium, Belarus, Czech Republic, Denmark, Estonia, Faroe Islands, Finland, Germany, Greenland, Iceland, Ireland, Latvia, Lithuania, Netherlands, Norway, Poland, Slovakia, Sweden, and Russia). In the NOBANIS network, Russia is represented as part of the shortened version of the database of alien species of the European part of Russia (NOBANIS 2021).

The full alien species database (DB) for the entire territory of Russia is registered in the international system Global Register of Introduced and Invasive Species (GRIIS), and published on the Global Biodiversity Information Facility (GBIF) portal (www.gbif.org) (Petrosyan et al. 2020a). The DB contains a list of 1,347 alien species from Russia. This list includes 19 taxa of alien species that have naturalized and are expanding their range (Petrosyan et al. 2017).

Despite the fact that there are general patterns in biological invasions and there are widely dispersed alien species, each country has its own particular features of invasions

and its own list of alien species, including the most dangerous (priority) species. In such a vast country as Russia, which covers an area of more than 17 million km^2 or about 1/8 of the Earth's land (Borodko 2020), invasions of many taxa occur at a large scale and require a comprehensive analysis of invasion patterns. Despite a great threat of biological invasions, there are not enough current, accurate data on the location of IAS in Russia. Although some regional or species/taxon-specific studies have been conducted (Alekseev 1989; Nedoluzhko 1997; Kuznetsov 2005; Berezina 2007; Bobrov et al. 2008; Vinogradova et al. 2009; Khlyap and Warshavsky 2010; Semenov 2010; Yakovleva and Yakovlev 2010; Kolyada 2011; Maslyakov and Izhevsky 2011; Kuzmin 2012; Antonova 2013; Gninenko et al. 2014; Ilyukh 2014; Kosoy et al. 2015; Devyatova et al. 2016; Ebel et al. 2016; Cherpakov 2017; Kukushkin et al. 2017; Karpun 2019; Khlopkova et al. 2019; Kudaktin and Romashin 2019; Petrosyan et al. 2019b; Shiganova et al. 2019; Khlyap et al. 2021a, b), a comprehensive database of occurrence records of invasive species is lacking at the national level.

A list of the 100 most dangerous IAS that pose a great threat to ecosystems and human health in Russia was published in 2018 (Dgebuadze et al. 2018). The main criteria (serious impact on biodiversity and human health at the local and regional levels) used for selection of the TOP-100 IAS among 1,347 alien species are presented in Suppl. material 1: TOP-100 selection criteria (DAISIE 2009; Dgebuadze et al. 2018). The TOP-100 Russian IAS include representatives from six kingdoms: Bacteria, Chromista, Fungi, Plantae (vascular plants), Protozoa (alveolates), Animalia (ctenophores, nematodes, molluscs, arthropods – crustaceans and insects, chordates – ascidians, ray-finned fishes, amphibians, reptiles, birds and mammals). The description of each species from the TOP-100 list is given in Dgebuadze et al. (2018), and includes species taxonomic position, the main species name and synonyms, native (historical) and invasive parts of the range, habitats, biology, its impacts on native species, ecosystems and humans, control methods, and geographical maps of its distribution. Despite the importance of the publication of the TOP-100 IAS, many aspects of the invasion process are not available in this book (Dgebuadze et al. 2018). In particular, it does not contain the diversified modern data analysis to assess the potential threat of IAS impacts on ecosystems including actual SOR, species distribution models (SDMs) and information about number of dangerous invasive species in different regions of Russia.

To fill these gaps, we created a database of SOR to identify the regions where IAS have been established in Russia. Construction of SDMs allows us to identify environmentally suitable regions for IAS, and thereby to predict potential risks of invasions (Wiens et al. 2009; Guisan et al. 2014). These models also help assess the risks of invasions of IAS and identify areas where alien species can potentially introduce, establish, spread and cause significant damage (Beukema et al. 2018).

The objectives of this research were to (1) create databases of species occurrence records for the TOP-100 IAS in Russia; (2) establish pathways, time of introduction and rates of accumulation of the TOP-100 IAS in Russia; (3) reveal the main types of spatial distributions of invasive species and their relationship with residence time; 4) distinguish regions with the highest IAS diversity and perform hot spot analysis of current distributions based on SOR.

Materials and methods

Assessment of the parameters of the species invasions

Taxonomic diversity and ecological groups of IAS

In total, we identified 1,347 alien species in Russia from which we selected the TOP-100 most dangerous IAS (see Introduction). We studied this TOP-100 IAS in Russia using a factographic database (**FDB**) of alien species. We regard the database of alien species as a factographic database because it is used for the collection and storage of important "facts" about each invasive species, including year of introduction, pathway of introduction, impact mechanism, impact output, native range, donor territory, etc (Suppl. material 2). We grouped the 100 species according to their taxonomy into 16 different taxonomic ranks: Bacteria (two species), Chromista (three species), Fungi (three species), Alveolata (one species), Vascular plants (29 species), Ctenophora (one species), Nematoda (two species), Mollusca (12 species), Crustacea (12 species), Insecta (15 species), Ascideacea (one species), Actinopterygii (five species), Amphibia (one species), Reptilia (one species), Aves (two species) and Mammalia (ten species) (Suppl. material 3).

In addition, we divided the species into five ecological groups: "microorganisms" (bacteria, chromists, fungi, alveoli, nematodes, 11 species), plants (vascular plants, 29 species), aquatic organisms (ctenophores, mollusks, crustaceans, ascidia, ray-finned fish, 31 species), terrestrial ectotherms (insects, amphibians, reptiles, 17 species) and endotherms (birds and mammals, 12 species).

Pathways, and accumulation rates of introduction, impacts of IAS on biodiversity and various sectors of the economy

The FDB of the TOP-100 species was used to assess parameters of the invasion process, including pathways of introduction, description of the native range, and to catalog which IAS have multiple impacts on hydropower, agriculture, forestry, fisheries and hunting area and human health. We also used FDB to estimate the accumulation rate of the TOP-100 IAS in Russia over time. The main trends in IAS introductions were determined based on the first record of establishment for each species in Russia. We used these data to construct regression model describing the dynamics of the number of IAS introductions over time.

Methods for constructing spatial distribution models (SDMs) using MaxEnt

The analysis consisted of four stages: (1) collection of vector database of species occurrence records and raster data of environmental variables; (2) selection of environmental variables and minimizing spatial autocorrelation (**SAC**); (3) assessment of the optimal parameters of the maximum entropy (**MaxEnt**) models according to the Akaike information criterion (**AICc**); and (4) construction of species distribution models (**SDMs**) using the MaxEnt method.

Collection of vector database of SOR and raster data of environmental variables

A vector database (VDB) was created in ArcGis Desktop 10.6.1 (ESRI 2017) using our original field data on SOR in combination with literature sources and museum collections, mainly from the Zoological Museum of MV Lomonosov Moscow State University, the museum of the Zoological Institute, Russian Academy of Sciences, DP Syreishchikov Herbarium of Moscow State University, Depository of Living Systems "Noah's Ark" of Moscow State University, and the Herbarium of the Botanical Institute of the Russian Academy of Sciences. Species occurrence records of the TOP-100 Russian IAS in North and South America, New Zealand, Western Europe, Southeast, South and Central Asia were obtained from the Global Biodiversity Database (**GBIF**) (www.gbif.org), Centre for Agriculture and Bioscience International (**CABI**) (www.cabi.org), Ocean Biodiversity Information System (**OBIS**) (obis.org), International Union for Conservation of Nature (**IUCN**) (www.iucnredlist.org), AquaMap (www.aquamaps.org), and early detection and distribution mapping system (www.eddmaps.org). SOR were collected from scientific papers and/or international sources of open access. We distinguished three types of SOR. The first type contained SOR described by accurate geographic coordinates. For this data type we first removed duplicates, and then we applied accuracy control filters (i.e. SOR that had accuracy of location of more than 5 km were excluded). Several taxa included in the TOP-100 list have subspecies rank. In this case, the SOR of the subspecies not listed in the TOP-100 were excluded. The second type included SOR whose locations are depicted in the maps without indicating accurate coordinates. For this type of data, geographic coordinates were identified using basemaps of Russia by procedures of geo-registration and binding the available species localities to basemaps using at least 30 control points chosen in the ArcGis Desktop 10.6.1 environment. Basemaps were obtained from Natural Earth of public domain map datasets (https://www.naturalearthdata.com/downloads/10m-cultural-vectors/10m-admin-0-countries). For the third type of data, we used only SOR that allowed us to determine the accurate geographic coordinates using GoogleEarth (earth.google.com) with an accuracy of at least 5 km.

We obtained a final set of SOR data by combining all three types of records after excluding duplicate records for species locations. Each SOR contained data collected over a period of twenty years (for some species, such as the *Apodemus agrarius*, over a period of 80 years) during which the species geographical distribution have been studied including species identity, accurate geographic coordinates and year of the first record. In total, there were 169,679 SOR, of which 100,613 were from the native part of the IAS range and 69,066 were from the invasive range (Suppl. material 3).

Spatial bioclimatic variables (**BIOCLIM**) with the numbers from 1 to 19 (Bio1–Bio19) were taken from a global dataset WorldClim 2.1 (http://worldclim.org/version2) with a resolution of 2.5 arc minute (~ 5000 m) (Fick and Hijmans 2017) for the historical climate. We used layers on a global scale because the native habitats of the TOP-100 IAS in Russia are located all over the world, including North and South America, New Zealand, North Africa, and Eurasia (Suppl. material 3). BIOCLIM variables characterize annual trends, seasonality, and fluctuations of temperature and

precipitation that commonly affect species distributions (Root et al. 2003; Bellard et al. 2013). In the case of freshwater species, many studies indicated strong correlations between spatial structures and climatic variables (Jocque et al. 2010), mainly temperature and water access. BIOCLIM variables were used to construct SDMs for various near-water and freshwater species (Drake and Bossenbroek 2004; McNyset 2005; Bellard et al. 2013; Banha et al. 2017).

In addition, we created raster layers of environmental variables in marine environments using the MARSPEC databases (Ocean climate layers for marine spatial ecology) (Sbrocco and Barber 2013). These layers are required for construction of SDMs of marine species. MARSPEC databases contain information related to the topographic complexity of the seabed, sea surface temperature and salinity. All raster layers of environmental variables BIOCLIM and MARSPEC datasets were prepared with resolution of 2.5 arc minute in *.asc and *.geotif formats.

Selection of environmental variables and minimizing SAC

The selection of variables for the modeling was carried out using a two-step procedure. At the first step, we created raster layers for the model-training regions for each environmental variable using the BIOCLIM or MARSPEC datasets. The model-training regions were described by the minimal convex polygons that included occurrence records reported for the native and invasive ranges (Rodda et al. 2011). The training areas were chosen based on the native and invasive regions of the species location including Russian regions (European part of Russia, Asian part of Russia – Ural, Siberia, Far East), regions of North America, Central and northern parts of South America, Western Europe, Central, Eastern, South Asia. At the second step, variables from the two sets of data, BIOCLIM and MARSPEC, were tested. We then selected variables for models using the ENMtools R-package (Warren et al. 2010). Those variables between which the pairwise Spearman correlation coefficient was greater than 0.75 in absolute value were excluded. Multicollinearity was assessed by the VIF (Variation Inflation Factor) using the Usdm R-package (Naimi et al. 2014). The advantage of the Usdm package for VIF assessment was described by Guisan et al. (2017). The environmental variable was regarded as multicollinear and excluded from the model if VIF > 5 (Hair et al. 1995; Guisan et al. 2017).

This two-step procedure led us to select six environmental variables from the BIOCLIM (Fick and Hijmans 2017) and MARSPEC (Sbrocco and Barber 2013) databases, which were used to construct SDMs for land (terrestrial and freshwater) and marine species, respectively. Environmental variables from the BIOCLIM set involved Bio1 (annual mean temperature), Bio5 (max temperature of warmest month), Bio11 (mean temperature of coldest quarter), Bio12 (annual precipitation), Bio13 (precipitation of wettest month), Bio14 (precipitation of driest month). Environmental variables selected from the MARSPEC dataset included Bathymetry (depth of the seafloor), Biogeo05 (distance to shore), Biogeo08 (mean annual sea surface salinity), Biogeo11 (annual range in sea surface salinity), Biogeo13 (mean annual sea surface temperature) and Biogeo16 (annual range in sea surface temperature).

There is no well-established methodology for accounting for SAC to build models based on only occurrence records (i.e. presence-only data) (Elith and Leathwick 2009; Guisan et al. 2017). We used an approach which involved random filtration of SOR to establish minimum spatial distances between the records (De Marco et al. 2008; Nuñez and Medley 2011; Marcer et. al. 2012; Václavík et al. 2012). Afterwards, we tested for SAC of model residuals. Many IAS have a large number of SOR. Therefore, they differ by spatial density depending on the number of samples collected in the native and invasive ranges. For this reason, we selected SOR using the procedure of random filtration of subsamples using the spThin package (Aiello-Lammens et al. 2015). This procedure is designed to (1) decrease the spatial bias of SOR located in different parts of the species range and (2) reduce the SAC of residuals of the model using approaches described by Dormann et al. (2007). We prepared two groups of datasets for each species. The first group of datasets included all available SOR without filtration. The second group consisted of 17 datasets, each of which included randomly selected SOR with different minimum distances. For the creation of these datasets we used minimum spatial distances in the range from 35 to 595 km at 35 km step. The MaxEnt models (stages three and four see below) constructed using these datasets were then tested for significance of autocorrelation of model pseudo-residuals (1 – probability of occurrence generated by model) by calculating Moran's I at multiple distance classes via the Ape (Paradis and Schliep 2019) and LetsR (Vilela and Villalobos 2015) packages. The significance was determined using permutation tests (Vilela and Villalobos 2015). We further used only those models that had a P-value greater or equal to 0.05.

Determination of the MaxEnt models' parameters

Although the MaxEnt default parameters for SDM are based on a large set of empirical data (Phillips and Dudik 2008), recent studies have shown that these models can be ineffective (Radosavljevic and Anderson 2014; Halvorsen et al. 2016). For this reason, we used three threshold-independent evaluation metrics: AUC_{Test}, AUC_{Diff}, and the Akaike size-adjusted information criterion (AICc) to select optimal MaxEnt parameters using the R-package ENMeval (Muscarella et al. 2014). AUC_{Test} is a metric that measures the discriminatory ability of a species distribution model using SOR that were not included in model construction. AUC_{Diff} is the difference between the AUC, calculated from the AUC_{Train} of the training set and AUC_{Test}. This metric (AUC_{Diff}) is a measure of the overfitting of the model. High AUC_{Diff} values characterize the degree of overfitting of the model (Warren and Seifert 2011). AICc – Akaike information criterion adjusted for small sample size reflects the degree of goodness-of-fit and complexity (Guisan et al. 2017). The model with the lowest AICc value is assumed to be the most appropriate model among the set of possible models. To estimate AUC metrics, we separated the calibration and evaluation SOR using the geographically structured partitioning scheme proposed by Radosavljevic and Anderson (2014) and implemented in the ENMeval R-package (Muscarella et al. 2014) (Suppl. material 4). This SOR partitioning scheme leads to more realistic and less biased estimates of SDM performance than the more traditional partitioning scheme using random k-fold. The

scheme of geographically separated SOR to determine the MaxEnt parameters is quite effective (Title and Bemmels 2018).

The ENMeval package created a series of MaxEnt models for each dataset using different regularization values and feature classes, compared them using the AICc criterion, and selected the most appropriate model. This package commonly selects a model that is less complex than the default model accepted by MaxEnt with an acceptable value of AUC_{Diff} metric (Halvorsen et al. 2016; Title and Bemmels 2018).

Construction of species distribution models (SDMs) using MaxEnt

The final IAS distribution models (**SDMs**) adapted to the historical climatic conditions were built using package MaxEnt 3.4.1 (Phillips et al. 2006) and Biomod v.2.0 R-package (Thuiller et al. 2021). The procedure for the selection of optimal parameters for these models was described above. SDMs were created as a result of 10 MaxEnt runs to randomly select test and training samples. Seventy percent (70%) of the SOR in the MaxEnt runs were used as training samples, and 30% of the records were used for testing models. For calibration of the model, we used from 1,000 to 10,000 randomly generated pseudo-absence (**PA**) points based on the number of SOR. We used a combination of the 'random' and 'sre' strategies for the generation of the PA points using the Biomod v.2.0 R package. Number of PA points was generated (as recommended by Barbet-Massin et al. 2012) according to the number (**N**) of SOR (if $N \leq 1000$ then 1000 points were selected, else 10,000 were selected).

We assessed the model performance using the Boyce (B_{ind}) index (Boyce et al. 2002; Hirzel et al. 2006) with the Ecospat R-package (Cola et al. 2017). Boyce index lacks several of the drawbacks associated with AUC index (Lobo et al. 2008). It requires only data on SOR and measures how much the predictive models differ from random distributions. The advantages of using this index have been shown in several studies (Hirzel et al. 2006; Petitpierre et al. 2012; Bellard et al. 2013; Petrosyan et al. 2019a, 2020b). We calculated B_{ind} for each of 10 model runs for each species, and then we averaged the run values to get the final estimates. The rank of each environmental variable in the SDM was estimated based on analysis of variable contributions and the jackknife method using MaxEnt. The highest rank was attributed to those environmental variables that had highest contribution in the model, i.e. had high values (> 5%) of permutation importance (**PI**) and/or high percent contribution (**PC**) (Phillips et al. 2006).

At this stage, we selected a model with $B_{ind} > 0.7$ and with insignificant SAC of residuals to compare it with the other models (see Selection of environmental variables and minimizing SAC section). If the model was accepted in terms of residuals, it was projected to the whole territory of Russia.

Assessment of actual and potential IAS invasive ranges in Russia

The first metric was evaluated using SDM, indicating environmentally suitable habitats for the introduction of the species in Russia, i.e. the potential invasive range. The

second metric obtained based on SOR specifies the regions where a species has already established. We assessed the size and geographical position of the invasive range by the number of administrative divisions of Russia: regions (oblasts), territory (krajs), republics, autonomous okrugs, autonomous oblasts and 2 cities of federal significance Moscow and St. Petersburg. The regions differ because they have different histories and/or types of administrative management. The map of Russian regions and the corresponding vector polygons (shape file) were downloaded from the Open Street Map source (www.openstreetmap.org).

Potential invasive range estimated by SDMs

First, we binarized the original SDM maps for the analysis. We transformed the probabilistic maps obtained with help of MaxEnt into binary suitable/non-suitable maps using the threshold maximizing the True Skill Statistics (**TSS**) (Guisan et al. 2017). Afterwards, we used the vector layer of geographic coordinates of the administrative regions of Russia to find the number of environmentally suitable regions for potential species invasion, using the "Extract Value" function in ArcGis Desktop 10.6.1.

Actual invasive range obtained based on SOR

To obtain the actual range of invasion, we converted vector polygons of the Russian regions (including coastal areas of the seas) into raster giving unique numbers to each polygon. From this, we then determined the regions which contained at least one occurrence record. Raster binary maps of the species occurrences were created for each species in the regions of Russia. Further, using the vector layer of geographic coordinates of the administrative regions of Russia, we found the number of regions where each species has been already naturalized using the "Extract Value" function in ArcGis Desktop 10.6.1.

Hereafter we used three categories to interpret the type of the distribution of species based on the SOR – local, regional, and wide. Species with local distributions occurred relatively close to the sites of introduction and were established in less than 33% of the regions of Russia. Species occupying more than 33% but less than 66% of the regions of Russia were considered as regionally distributed. Species with wide distributions had almost continuous distributions colonizing more than 66% of the Russian regions from the western to eastern borders of Russia.

Assessment of IAS richness in different Russian regions

IAS richness

To find the actual number of IAS, we summed the created raster binary maps showing occurrence sites of species. Afterwards, we obtained the final raster map of the species richness in different Russian regions using the R-package raster. We then created a vec-

tor map of species richness in Russian regions for hot/cold spots analysis using the final raster map of IAS richness and vector layer of geographic coordinates of the centers of Russian administrative regions.

Hot spots analysis and zoning according to assessments of IAS impact on ecosystems

To identify zones with high impacts of the most dangerous IAS on Russian ecosystems, we used an analysis of hot and cold spots and a procedure of constructing kernel density in the ArcGis Desktop 10.6.1 environment. Hot, cold and neutral spots were identified based on the Getis-Ord Gi * statistic (Andy 2005) using Z-scores and P-values. As a result, we identified three types of zones distinguished by IAS richness that we regard as a proxy of IAS impacts. The first type of zone aggregates hot spots with the highest richness of IAS, which, consequently, have a great impact on ecosystems. The second zone type aggregates cold spots indicating regions with few invasive species that have reduced impact. Neutral zone type does not belong to the above two types and are characterized by intermediate richness and intermediate impact on ecosystems. Finally, we constructed the original map of hot/cold spots with Russian territory zoning according to assessments of IAS impact on environmentally suitable ecosystems.

We constructed SDMs using R (R-version 3.6.2 2019) and R-packages Ape (Paradis and Schliep 2019), Biomod2 (Thuiller et al. 2021), Dismo (Hijmans et al. 2017), Raster (Hijmans et al. 2020), Ecospat (Cola et al. 2017), ENMeval (Muscarella et al. 2014), ENMtools (Warren et al. 2010), SpThin (Aiello-Lammens et al. 2015), LetsR (Vilela and Villalobos 2015) and Usdm (Naimi et al. 2014). In addition, we applied R-scripts presented in Hirzel et al. (2006) to assess the suitability of models using RSTUDIO v. 1.4.1106 software (RStudio 2020). The analysis of hot/cold spots, construction of the kernel density of hot/cold spots and visualization of the SDMs were conducted in the ArcGis Desktop 10.6.1 environment (ESRI 2017).

Results

General description of the database of SOR

The TOP-100 IAS of Russia were represented by 16 taxonomic groups (Suppl. material 3), of which 78 species were found in five groups: vascular plants – 29, insects – 15, molluscs – 12, crustaceans – 12 and mammals – 10 species. The other 11 taxonomic groups include only 1–5 species each (Fig. 1). We identified 169,709 SOR for the TOP-100 IAS in their native and invasive ranges, which included 1,117 for bacteria, 2,448 for chromists, 2,350 for fungi, 87,497 for vascular plants, 1,371 for alveolates, 760 for ctenophores, 407 for nematodes, 12,855 for molluscs, 11,995 for crustaceans, 3,780 for insects, 419 for ascidians, 14,746 for ray-finned fish, 5,197 for amphibians, 1,762 for reptiles, 2,279 for birds and 20,726 for mammals (Fig. 1). The number of SOR for individual species in their invasive and native ranges is presented in Suppl. material 3.

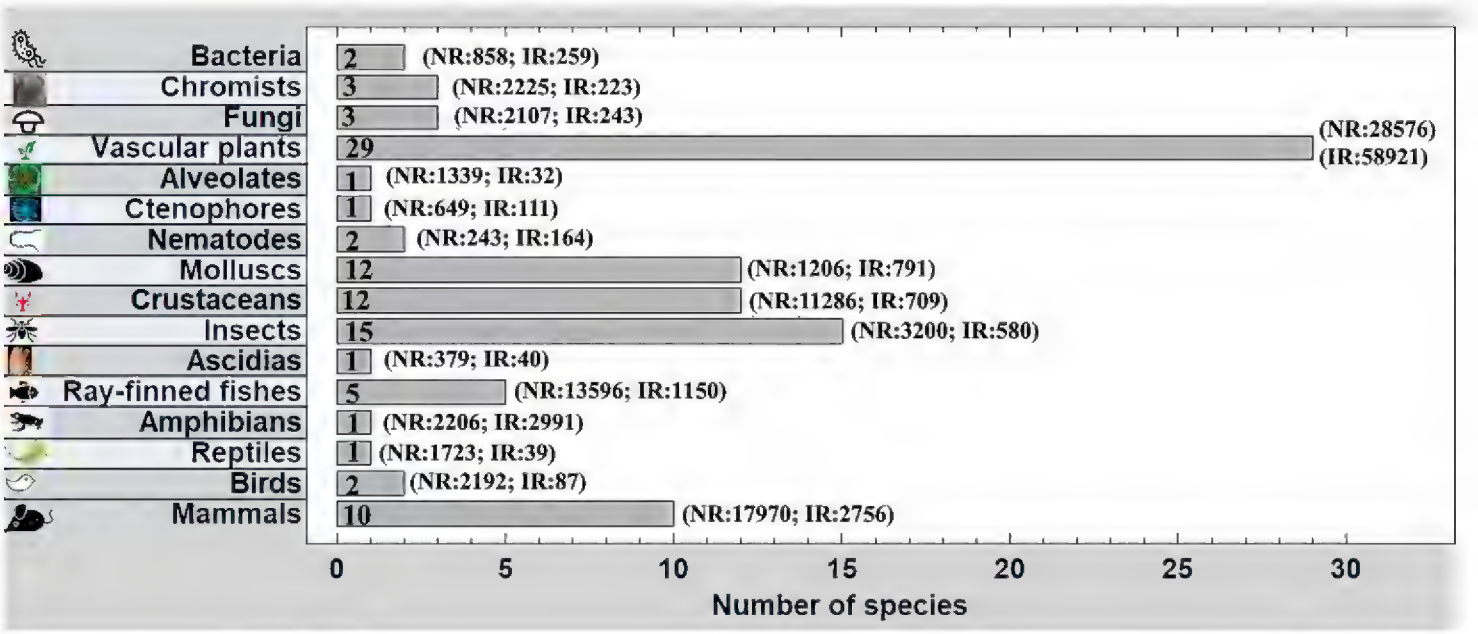

Figure 1. Species occurrence records (SOR) in the native and invasive ranges of the TOP-100 IAS in Russia, which were used to assess actual and potential IAS invasive ranges. The number of species in each of 16 taxonomic groups is indicated in the grey bars; NR and IR are the numbers of SOR in the native and invasive ranges, respectively.

The number of SOR varies widely between ecological groups. The highest number of SOR (58,921) was recorded in plants, which consists of 29 species. Most of the plant species have colonized natural, disturbed, and/or urbanized terrestrial and aquatic ecosystems in Russia (Vinogradova et al. 2009, 2018; Vinogradova and Kupriyanov 2016). American maple (*Acer negundo*) has the highest number of SOR (8,849). All occurrence records for this species of maple are located in the area from the western (including Kaliningrad Region) to the eastern borders of Russia.

A total of 3,610 SOR were reported from 17 species of terrestrial ectotherms, 3,231 SOR from 31 species of aquatic organisms, and 2,413 SOR from 11 species of terrestrial endotherms. Within these ecological groups, the highest number of occurrence records (2,691) was reported for the marsh frog (*Pelophylax ridibundus*), which are located in the southern Ural, Siberia and Kamchatka (Kuzmin 2012). The lowest number of occurrence records (921) was found for 11 species of "microorganisms". Such a low number of SOR for "microorganisms" was mainly attributed to the hard detection and species identification relative to representatives of the other groups. The highest number of records (208) in this group was reported for wetwood (*Pectobacterium carotovorum*) which were registered in all the forest areas on Russian territory except for the cold regions of Siberia (Cherpakov 2017).

Geographical IAS origin and pathways of their introduction

The greatest number of invasive species originated from America (45 species), which included North America (31 species), Central America including Mexico (3 species) and South America (2 species), the western coast of these continents with adjacent waters of the Atlantic Ocean (8 species) and the eastern coast and the Pacific Ocean

(1 species) (Suppl. material 3). One species (*Potamopyrgus antipodarum*) originated from New Zealand. *Cylindrospermopsis raciborskii* originated from either African or Australian. We were not able to establish the origins of 10 species. The native ranges of the rest of the TOP-100 IAS (43 species) were Eurasia and its surrounding waters. IAS from East Asia contributed the second most IAS to Russia (18 species). Native ranges of three species were located in Southeast Asia; two species originated from the north of the Pacific Ocean and adjacent land. Two terrestrial and one marine species invaded Russia from the south of Eurasia, two species invaded from Europe, two species came from Central Asia, and one species from the Caucasus. The Ponto-Caspian Basin was an important source of aquatic IAS (6 species) (Suppl. material 3). Among the aforementioned groups of Eurasian species, the range of 31 species at least partly includes the territory of Russia. Species living in East Eurasia, including the Russian Far East, as a rule, did not expand their range westwards but they invaded into Russian regions through Western Europe.

We found that 62% of the TOP-100 IAS were introduced into Russia unintentionally (accidentally), a third (33%) were intentionally introduced, and 5% invaded mainly by self-dispersal. The list of the TOP-100 is mainly represented by IAS carried to Russia with ballast water (22 species), cultivated plants (16 species), fouling of ships (11 species), and traffic flows (10 species).

Dynamics of accumulation of invasive species over time

The dynamics of the number of introduced IAS over time showed that there was a nonlinear relationship between the number of invasive species and year of introduction from 1600 to 2018 ($F = 2138$, $P << 0.01$, $R^2 = 98\%$) (Fig. 2, Suppl. material 3). The number of IAS that invaded Russia started to grow sharply in the middle of the 20th century. As such, the introduction of 52% of the species from the TOP-100 list occurred over a 76-year period from 1946 to 2018. Moreover, we found a significant difference ($Z = 9.5$, $P << 0.01$) in the rates at which new species were introduced (Rsy) between the two periods, namely, 1600–1945 (Rsy = 0.14 species/year) and 1946–2018 (Rsy = 0.65 species/year) (Fig. 2).

General characteristics of the impact of IAS on biodiversity and various sectors of the economy

We compiled a list of invasive species that have the greatest impact on biodiversity, various sectors of the economy, and human health (Fig. 3). Among the TOP-100 species, 36 species displace native species and 37 significantly alter the ecosystem (Fig. 3A). Seventeen species compete with native species and/or are able to displace them and five species are involved in hybridization processes. Thirty-seven species have great impacts on human health and eight species have considerable effects on hydropower systems. Some species are harmful for agriculture (29 species), forestry (20 species), fishery (13 species) and hunting grounds (8 species) (Fig. 3B).

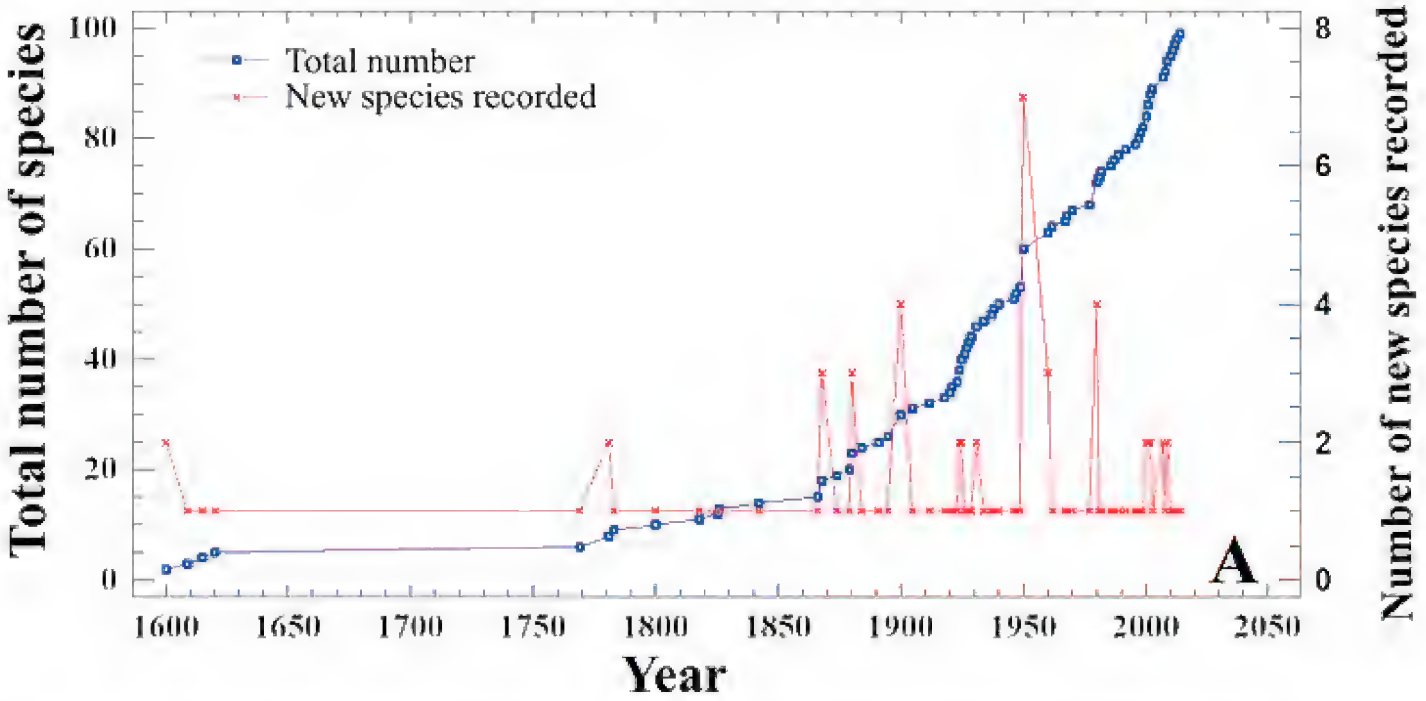

Figure 2. Number of IAS introduced during 1600–2018 in Russia (panel **A** – red) and accumulated number of species (AS) (panel **A, B** – blue dots). In the panel **B** blue curve shows nonlinear trend AS = exp (-5.73 + 0.000002536* Years^2); red lines depict 95% confidence intervals.

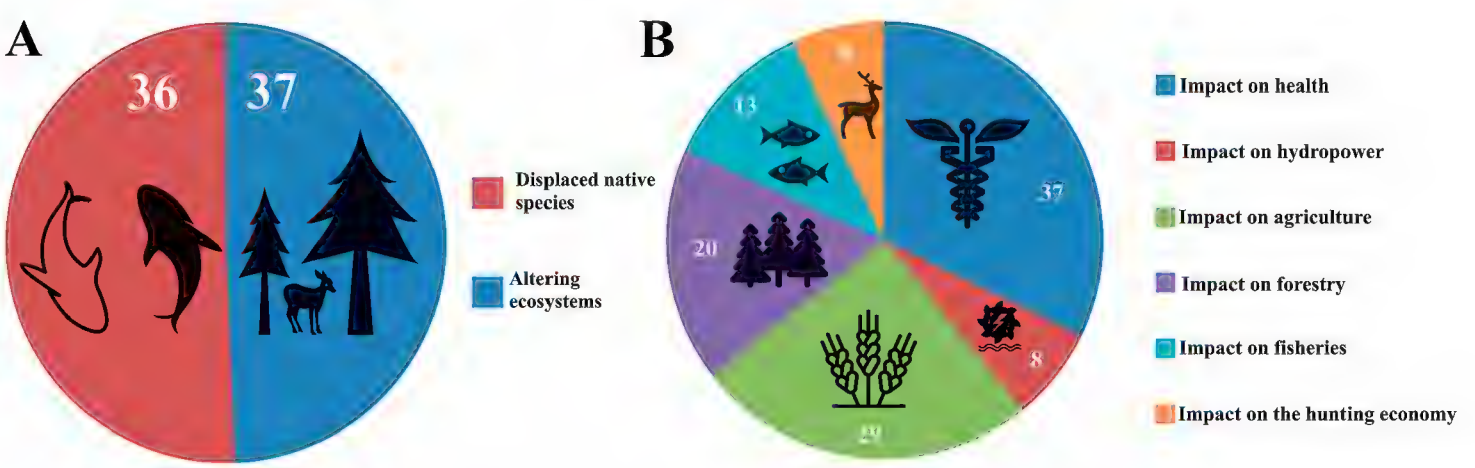

Figure 3. Impacts of the TOP-100 IAS on biodiversity, economic sectors, and human health in Russia. Panel **A** shows number of IAS altering ecosystems and displaced native species **B** shows impacts of IAS on economic sectors in Russia.

Species distribution models (SDMs)

After random selection of occurrence points, the minimum distances between the SOR points ranged from 133 to 555 km, depending on the degree of SAC for each species. This procedure reduced the number of SOR by 88%, eliminated spatial sample bias and SAC of residuals (Suppl. material 5). Furthermore, it created similar distributions of SOR in the native and invasive ranges. Moran's I correlograms for different distance classes did not show any SAC in the residuals of any of the models (Suppl. material 6). The reduced SOR data and six environmental variables from each dataset were used to construct SDMs. These models demonstrated high performance in terms of the B_{ind} index which varied from 0.76 to 0.99 with the mean 0.94 (Suppl. material 7). Based on SOR and SDMs, the studied species were divided into three groups according to their type of distribution, specifically, species with local, regional and wide distributions (Suppl. material 7). Suppl. material 7 includes short descriptions of IAS current distributions in Russia based on SOR, in particular, the number of regions in which species have already established or can potentially invade, the types of actual and predicted species distributions and model performance metrics (Boyce index – B_{ind}). Most of the IAS (56 species) currently have local distributions, slightly less (26 species) are distributed regionally, and even fewer (17 species) have wide distributions. MaxEnt models predicted a local distribution for 48 species, a regional distribution for 31 species, and a wide distribution for 20 species. Thus, SDMs predicted a decrease in the number of species (by 8) with a current local regional distribution and an increase in the number of species (by 5) with regional and wide distributions (3), respectively. The species with the widest distribution from each of 16 taxonomic groups (Suppl. material 7) are represented in Fig. 4.

The maps in Fig. 4 show that among 16 species, MaxEnt predicted local distributions for four species (Fig. 4E, F, K, N), regional distributions for seven species (Fig. 4B, C, H, I, J, M, O), and wide distributions for five species (Fig. 4A, D, G, L, P). Suppl. material 7 based on SOR data shows that among 11 less numerous species taxa, 16 IAS currently have local distributions, two species have regional distributions, and four species have widespread distributions. However, species distribution patterns are different in taxa that have a large number of IAS. In particular, a large proportion of invertebrate species have local distributions (90%), while a large proportion of vertebrate species have wide distributions (56%). For plants, the majority (66%) of species have regional distributions. A total of 78 (± 16)% of the potentially suitable regions for invasion in Russia have already been occupied (Poc) by IAS as predicted by SDMs. For species with local, regional and widespread distributions, the Poc values showed that 69 (± 15)%, 87 (± 6)% and 93 (± 4)% of potentially suitable regions had been naturalized, respectively. Thus, the largest portion of potential expansion area into environmentally suitable regions is predicted for species with local distributions (31%) and the smallest percentage of potentially expansion area is expected for species with widespread distributions (7%). For species with regional distributions, the portion of species expansion area into suitable regions is intermediate (13%).

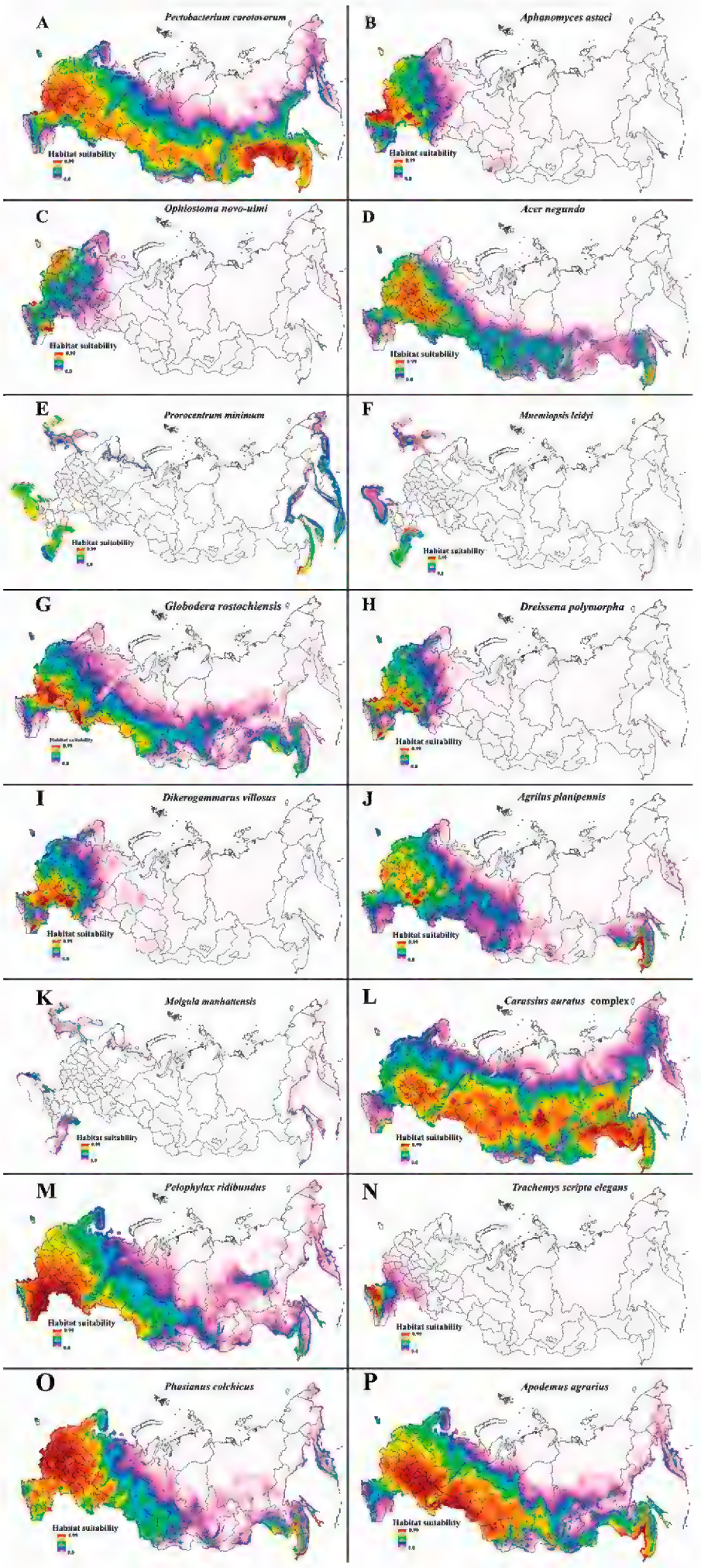

Figure 4. Predicted potential distributions of IAS including one species from the 16 taxonomic groups using SDMs. MaxEnt models used for prediction were optimized in terms of feature class and regularization according to the AICc metric. These models were constructed using selected environmental variables from the BIOCLIM or MARSPEC datasets, where species in the panels **A, D, G, L, P** have wide distribution, species in the panels **B, C, H, I, J, M, O** have regional distribution and species in the panels **E, F, K, N** have local distribution. Marine species and sea areas are shown in **E, F, K**.

Species occurrence records identified a positive relationship between the time since introduction and the type of distribution (either local, regional, or widespread), which was assessed by Spearman's rank coefficient (Src = 0.58, P << 0.01). Species with local (56 species), regional (26 species), and widespread distributions (17 species) were introduced on average 55 (± 5), 126 (± 8), and 190 (± 12) years ago, respectively. This average residence time for species with a widespread distribution is likely an underestimate because there are IAS that were introduced before the 16th century (Suppl. material 3).

SDMs showed that the environmentally suitable habitats for IAS with local distributions are mainly located in the European part of Russia. Species with regional distributions are found in the European part of Russia (9 species) and simultaneously in the European and Asian parts of Russia (22 species). The environmentally suitable habitats for the IAS with widespread distribution are located in the European part, as well as in the Asian part of Russia (Suppl. material 7).

IAS richness in different regions of Northern Eurasia

We determined the IAS richness in each administrative division of Russian territory and adjacent seas, by overlaying the SOR on the polygonal raster map (Fig. 5, Suppl. material 8). The map shows that hot spots and zones with high concentration of IAS are located in the European part of Russia (Fig. 5). In the Asian part of Russia, only cold and neutral spots were found (Fig. 5). The maximum number of species was identified in hot spots A1 (64 species, Krasnodar territory), A2 (60 species, eastern coast of the Black Sea), A3 (55 species, Leningrad region), A4 (52 species, Rostov Region) and A5 (51 species, Moscow).

In the European part of Russia, we distinguished five zones with high concentrations of hot spots (Z1 – Z5). Zones Z1 and Z2 are located in the central part of European Russia and include 23 and 7 hot spots, respectively. Zone Z3 lies in Central Ciscaucasia and includes 7 hot spots. Two smaller zones (3 hot spots in each zone) are located northwest of the European part of Russia including the adjacent part of the Baltic Sea (Z4) and in the Northwestern Caucasus including the adjacent part of the Black Sea (Z5). Cold spots are located in the north-east of the European Russia and Asian Russia (Fig. 5, Suppl. material 8). Statistical significance levels of hot, neutral and cold spots of IAS included in the TOP-100 list are confirmed by GiZScore statistics.

Discussion

We combined data in one comprehensive national database on the most dangerous TOP-100 invasive alien species in Russia, which includes data on trends and pathways of invasions, and was used to identify regions of current and predicted IAS distributions. This database included SOR in accordance to taxonomic and location quality criteria, and data on the rate of IAS accumulation over time. Although our analysis involved only 100 invasive species (7.4%) out of 1,347 IAS reported in Russia (Petrosyan et al. 2020a), these species pose the greatest threat to biodiversity and human health.

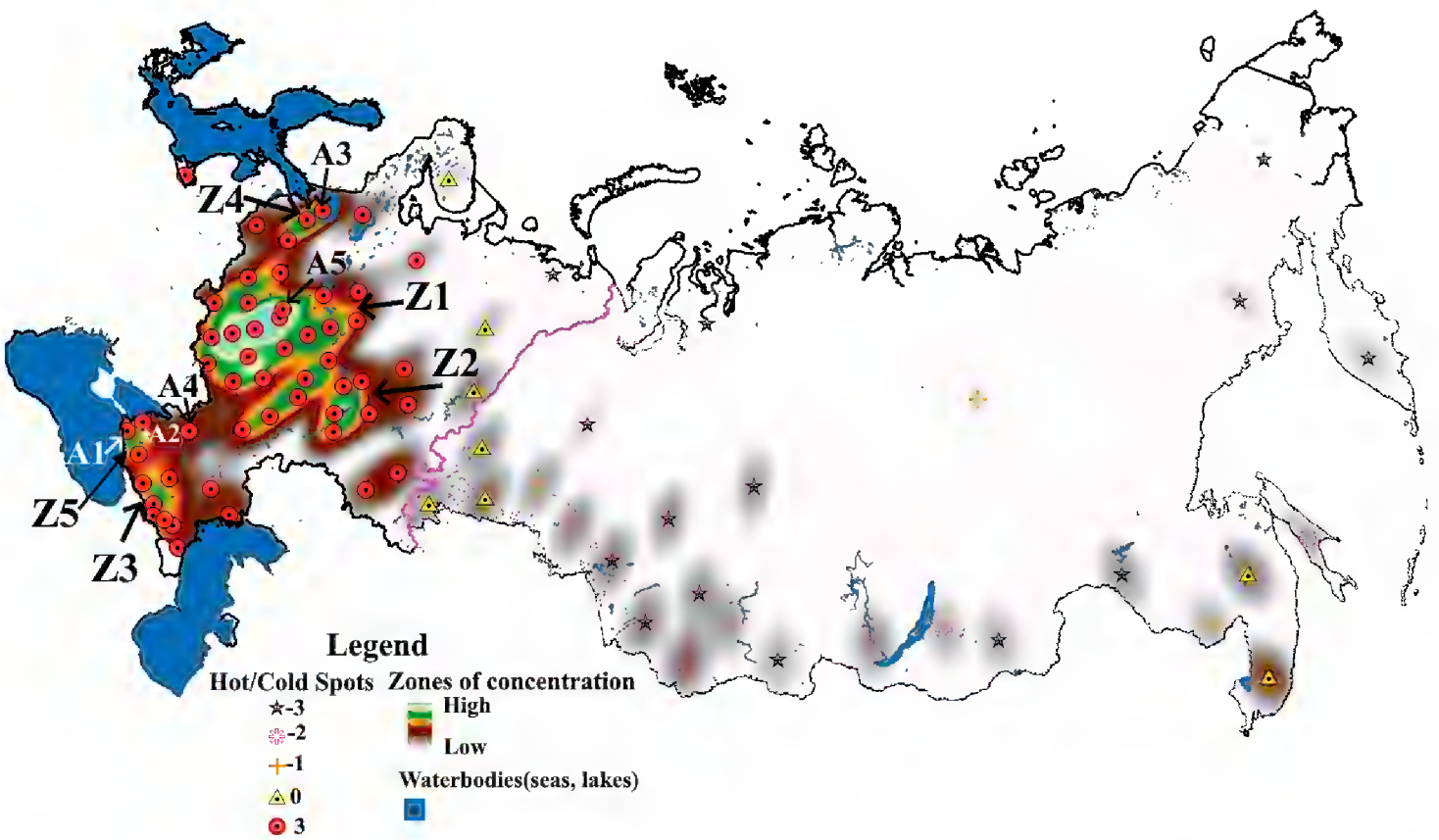

Figure 5. Hot/cold spots and zones of IAS impact on ecosystems. Cold spots with -3, -2, -1 bins reflect statistical significance with confidence levels of 99, 95 and 90% respectively, spots with 0 bins have no statistical significance. Hot spots with 3 bins reflect statistical significance with confidence levels of 99%. Symbol A denotes hot spots, symbol Z denotes zones with a high concentration of hot spots based on kernel density analysis procedure. The pink line indicates the border between the European and Asian parts of Russia.

Therefore, these species require special attention of scientists and decision-makers, which is consistent with the main objectives for the conservation of biological diversity Act before (Overview of outcomes 2011; Quick guide 2021) and after 2020 (Synthesis report 2019; Post-2020 global biodiversity framework 2020). Selection criteria for the TOP-100 in Russia (Suppl. material 1) are in full agreement with those used to identify the 100 most harmful species out of 11,000 alien species in Europe (DAISIE 2009). The TOP-100 list for Russia does not include quarantine invasive species (Kirichenko et al. 2021) because, according to Russian legislation, a quarantine species is a species that has not yet been introduced, but there is a risk of its introduction, or a species that has already been introduced but still has a limited distribution (On Plant Quarantine 2014). Species from the 1,347 species pool that were not included in the TOP-100 list either have limited distribution or their impacts on biodiversity and human health are not known. However, the invasion process is dynamic and priority IAS lists should be modified over time.

Occurrence records, invasion trends and pathways of the most dangerous IAS in Russia

The invasion process in Russia has a long history. Nevertheless, a non-linear upward trend in the dynamics of the total number of invaded species has been observed only since the late 1940s showing three peaks during 1946–1962, 1970–1981 and 2000–2014. Since

1946, the number of recorded IAS has doubled, and further increases are expected. A similar rapid growth in the number of invasive species has been documented in other countries since the second half of the 20th century, including Croatia (Nikolić et al. 2013), East Africa (Witt et al. 2018) and Romania (Sirbu et al. 2022). The above studies show that peaks in the numbers of newly introduced species occurred in Romania (Sirbu et al. 2022) and Croatia (Nikolić et al. 2013) in the 1950s, while in East Africa (Witt et al. 2018) and Russia, the maximum numbers of introduced species declined during 1940s–1960s. Common factors that facilitated the increase in introductions in the second half of the 20th century in Russia included increases in traffic flows (Kalabekov 2020) and interstate communications. Among the 14 species (represented in the TOP-100 list) that invaded Russia from 1946–1962, seven species were introduced with ballast water, fouling of ship hulls or accidentally with other aquatic organisms; four species were accidentally introduced via land routes (transport and shoots of plant culture); two species were intentionally introduced, and one species – *Castor canadensis* – invaded Russia independently from the territory of Finland.

Most of the TOP-100 IAS in Russia originated from North and Central America (45%), and the Asia-Pacific region (32%). A total of 62% of the IAS were unintentionally introduced, 33% were intentionally introduced and 5% were self-dispersed. The ratio of the number of unintentionally: intentionally introduced IAS is 1.82, which is higher than this ratio for invasive plant species in Europe (0.59) (Lambdon et al. 2008). Such a low ratio in Europe is related to the fact that the main pathways of introduction of invasive alien plant species (52% of the total number of invasive plant species in Europe) are dispersing through gardening and the use of alien plants for ornamental purposes. The horticultural industry, in particular, ornamental horticulture, is regarded as an important pathway for introduction and dispersal of alien species (Drew et al. 2010). In the TOP-100 list of IAS in Russia, the number of invasive species introduced with cultivated plants accounts for 16%. The TOP-100 list also includes a large portion of species introduced with ballast water, transport flows, ship fouling and agricultural products (58 species) (Petrosyan et al. 2017; Dgebuadze et al. 2018).

Current distribution of IAS

Local distribution

We showed that recently invaded IAS commonly have local distributions. Specifically, local distributions and a relatively short resident time of introduction are typical of 56 of the TOP-100 species (Suppl. material 7). This includes eight species of "microorganisms", three plant species, 28 aquatic species, 14 species of terrestrial ectotherms and three species of terrestrial endotherms. The mean residence time for these species is 55 (± 5) years (Suppl. material 3). MaxEnt models with high predictive accuracy according to the B_{ind} index (0.95 ± 0.04) indicated that there are 1–11 environmentally suitable regions for the potential invasion of most of the locally distributed species (Suppl. material 7). Only two aquatic species, namely, naval

shipworm (*Teredo navalis*) and red king crab (*Paralithodes camtschaticus*), were not predicted to expand further. These two species currently occupy all available coastal areas of the Black and Japan Seas (*T. navalis*) and the Barents Sea (*P. camtschaticus*) and their further dispersal may occur beyond Russian territorial waters.

Regional distribution

Among the TOP-100 IAS with regional distributions (26 species), the number of plant species (19 species) is the highest (Suppl. material 7). "Microorganisms" and aquatic organisms are represented only by one species each, and terrestrial ectotherms and endotherms include only two and three species, respectively. The mean residence time for these species is 126 (± 8) years (Suppl. material 3). MaxEnt models (B_{ind} = 0.92 ± 0.06) predict that environmentally suitable regions for potential invasions (Suppl. material 7) of IAS with regional distributions will increase by 2–11 new regions. In particular, "microorganisms" occupy six more regions, plants 3–11 more regions, aquatic organisms seven more regions, terrestrial ectotherms 5–11 more regions and endotherms 2–7 more regions.

Widespread distribution

The number of the TOP-100 species with widespread distributions is relatively small (17 species). Among them, plants had the highest number of species with widespread distributions (7 species) (Suppl. material 7). These species have similar geographical distributions and are found in all major regions of Russia, namely, the European part of Russia, the Urals, the southern parts of Siberia and the Far East. Widespread distribution was determined for two "microorganism" species and two aquatic species, one terrestrial ectotherm, and five terrestrial endotherms. The mean residence time for these species is 190 (± 17) years (Suppl. material 3). MaxEnt models (B_{ind} = 0.93 ± 0.06) predict that the number of occupied regions by widespread species will increase by 2–11, specifically, "microorganism" species will expand over 6 more regions, plants occupy 3–11 more regions, aquatic organisms 4–6 more regions, terrestrial ectotherms four more regions and endotherms 2–5 more regions.

SOR of 17 widespread species from the five taxonomic groups showed that this type of distribution is largely attributed to species that are ecologically tolerant to a large range of abiotic and biotic factors. There are also other reasons for successful distribution, including the absence of competitors, long residence time and a great variety of invasion pathways. In particular, the main pathways of plant introductions are associated with their use as ornamental plants in urban landscaping and forest belts, distribution with forage grasses, spread with ground and water transport, use in aquaculture and fishery and with the import of grain and animal food. In addition, many plant species are also dispersed by birds, small mammals and bears (Vinogradova et al. 2009, 2018; Vinogradova and Kupriyanov 2016). In general, the spread of plant invaders via anthropo- and zoochory has ensured a high level of propagule pressure that facilitates the wide geographical distribution of IAS plants (Vinogradova et al. 2009, 2018).

The vast range of the bacterium *P. carotovorum*, nematode *G. rostochiensis* and insect *L. decemlineata*, are attributed to the widespread distribution of their hosts and the high rates of development of forestry and agriculture (Butorina et al. 2012; Cherpakov 2017; Dgebuadze et al. 2018).

Dispersal of fish (*C. auratus*, *P. glenii*) and mammals (*N. vison*, *O. zibethicus*) have different patterns. They (fish and mammals) were introduced, often repeatedly, into many primary areas (Bobrov et al. 2008; Khlyap and Warshavsky 2010; Reshetnikov 2010; Vekhov et al. 2018). For example, two species of mammals (*N. vison*, *O. zibethicus*) were deliberately introduced as a fur resource. Approximately 19,000 American minks and more than 330,000 muskrats were released from 1928 to 1970 in different regions of Russia (Bobrov et al. 2008). Subsequently, these foci merged into a single vast range as a result of further self-dispersal.

Zoning of Northern Eurasia according to assessments of IAS richness

The identification of regions with the greatest IAS impacts on ecosystems is important for controlling IAS and forecasting potential regions of ecological disaster. We focused on administrative divisions of the Russian territory because the most important functions of nature management and environmental protection are implemented mainly by regional or republican services. Dangerous IAS occur in all regions of the Russian Federation. The greatest taxonomic diversity of IAS was found in the central part of European Russia, where the highest concentration of hot spots is observed (Z1). That is related to better civil development of the region and, consequently, greater anthropogenic transformation of this territory (Zubarevich 2010). The second most important zone of high IAS concentration is the Middle Volga region (Z2). After the construction of hydraulic structures linking the basins of the Baltic, Black and Caspian Seas into a single system, corridors of aquatic species spreading between the north (Baltic Sea) and the south converge in the middle reaches of the Volga (Slynko et al. 2002) to increase the number of IAS in this region. In our opinion, this invasion corridor contributed to form two hot spots in the Baltic (Z4) and Black Seas (Z5) regions. The increase in the concentration of hot spots in the south of European Russia (Z3 and Z5) is associated additionally with more favorable natural conditions for IAS, mainly with warmer climate. The identification of hot spots zones based on SOR would allow decision-makers to purposefully minimize threats from IAS, constrain their spread and/or eradicate IAS from the regional pool.

MaxEnt model predictions of IAS potential distribution

We followed best practices in model development (see in Fitzpatrick et al. 2006; Broennimann et al. 2007; Dormann et al. 2007; Kühn 2007; Beaumont et al. 2009; Guisan et al. 2014; Muscarella et al. 2014; Radosavljevic and Anderson 2014; Guisan et al. 2017; Petitpierre et al. 2017; Liu et al. 2020; Pili et al. 2020) to create SDMs for terrestrial, freshwater, and marine IAS. As a result, we were able to predict IAS

distribution with high accuracy and without SAC in the residuals. Therefore, we strongly suggest using SDM and associated maps to predict expansion of IAS ranges into suitable regions.

Further species dispersal to environmentally suitable regions in accordance with predictions of MaxEnt models, is highly probable because measures to prevent self-dispersal and/or to restrict abundance were applied only for 19 species from the TOP-100 IAS in Russia (Dgebuadze et al. 2018). Control methods have been developed for 62 species including mechanical, chemical or biological approaches. Yet, there are no control methods to constrain population growth for 38 species either in Russia or in the world (Clout and Williams 2009; DAISIE 2009; Isaev 2015; Dgebuadze et al. 2018).

Conclusions

Although there is a long history of species invasions in Russia, the number of introduced IAS has been growing non-linearly over the past 76 years. The TOP-100 list is represented by 62% species that were unintentionally introduced (imported) with ballast water, traffic flows, ship fouling, agricultural products, cultivated plants and plants for landscape design. Intentional introductions have contributed much less to the invasion of IAS in Russia (33%). The majority of IAS recorded in Russia originated from North and Central America (45%) and the Asia-Pacific region (32%).

The database of actual SOR in individual regions of Russia and SDM maps allowed us to distinguish three types of distributions of the TOP-100 IAS which included local (56 species), regional (26 species) and widespread (18 species) distributions. We found that species that are widely distributed in Russia were introduced more than 190 years ago, species that are regionally distributed appeared in Russia 126 years ago, and species that are locally distributed first arrived 55 years ago.

We identified zones with high concentrations of IAS where the potential impact of IAS on terrestrial and aquatic ecosystems was the highest. These zones are located mainly in the more developed parts of European Russia with strong trade links and in the southern warm regions including the coasts of the Black Sea. We propose regularly updating SOR databases that can serve as a valuable tool in the management of biological invasions at the national and regional levels. It is noteworthy that the database of SOR at the geopolitical/regional subjects' level and MaxEnt models can be used for estimating rates and dynamics of IAS dispersal.

Acknowledgements

We are thankful to many people for their efforts in collecting, aggregating and publishing data on alien species in Russia, especially to – Ivan Bashinsky, Nadezhda Berezina, Vladimir Bobrov, Vladimir Cherpakov, Polina Dgebuadze, Yuri Dgebuadze, Galina Finenko, Maria Gololobova, Alexandra Gubanova, Andrey Gusev, Daria Guseva,

Dmitry Karabanov, Lyudmila Korneva, Marina Krivosheina, Valentina Kuranova, Dmitry Kuznetsov, Alexander Mishchenko, Olga Morozova, Tatiana Morozova, Marina Orlova, Vladimir Oskolkov, Nadezhda Ozerova, Andrey Reshetnikov, Nikolay Revkov, Vyacheslav Rozhnov, Sergey Scarlato, Tamara Shiganova, Alexander Soldatov, Maria Sotskaya, Irina Telesh, Dmitry Vekhov, Yulia Vinogradova, Viktor Voronin, Yulia Zagorodnyaya, Anna Zalota, Svetlana Zinovieva, and Alexander Zvyagintsev. We are especially grateful to the subject editor, Helen Sofaer, and two anonymous reviewers, for their valuable suggestions on the manuscript. The study was supported by the RSF Project Nº 21-14-00123. The authors are also grateful to ESRI (USA) for providing a free-of charge licensed version of ArcGis Desktop 10.6.1 (ESRI Sales Order number 3128913; ESRI Delivery number 81833751, User customer number 535452).

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Supplementary material 1

Criterion selection of the TOP-100 IAS

Authors: Varos Petrosyan, Fedor Osipov, Irina Feniova, Natalia Dergunova, Andrey Warshavsky, Lyudmila Khlyap, Andrew Dzialowski

Data type: text (Pdf file)

Explanation note: The main criterion for selecting the TOP-100 invasive alien species (IAS).

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Link: https://doi.org/10.3897/neobiota.82.96282.suppl1

Supplementary material 2

General description and conceptual structure of the database (FDB)

Authors: Varos Petrosyan, Fedor Osipov, Irina Feniova, Natalia Dergunova, Andrey Warshavsky, Lyudmila Khlyap, Andrew Dzialowski

Data type: figure (Pdf file)

Explanation note: General description of the factographic database (FDB) of alien species in Russia and functional links between master and reference tables (fig. S1).

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Link: https://doi.org/10.3897/neobiota.82.96282.suppl2

Supplementary material 3

Species native range, introduction year, occurrence records

Authors: Varos Petrosyan, Fedor Osipov, Irina Feniova, Natalia Dergunova, Andrey Warshavsky, Lyudmila Khlyap, Andrew Dzialowski

Data type: table (xlsx file)

Explanation note: Species native range, introduction year in Russia, number of occurrence records in the native and invasive ranges and years of creation of datasets (sheet 1), DOIs of used datasets (sheet 2), full datasets of species occurrence records (sheet 3).

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Link: https://doi.org/10.3897/neobiota.82.96282.suppl3

Supplementary material 4

Geographic partitioning of the SOR

Authors: Varos Petrosyan, Fedor Osipov, Irina Feniova, Natalia Dergunova, Andrey Warshavsky, Lyudmila Khlyap, Andrew Dzialowski

Data type: figure (Pdf file)

Explanation note: Geographic partitioning of the SOR (using *Acer negundo* as an example).

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Link: https://doi.org/10.3897/neobiota.82.96282.suppl4

Supplementary material 5

Moran's I indexes of residual spatial autocorrelation for MaxEnt models

Authors: Varos Petrosyan, Fedor Osipov, Irina Feniova, Natalia Dergunova, Andrey Warshavsky, Lyudmila Khlyap, Andrew Dzialowski

Data type: table (xlsx file)

Explanation note: Moran's I indexes of residual spatial autocorrelation for MaxEnt models predicting the distribution of IAS in Russia and adjacent territories. These models were calibrated based on the SOR reported in the native and invasive range

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Link: https://doi.org/10.3897/neobiota.82.96282.suppl5

Supplementary material 6

Moran's I correlograms of residual spatial autocorrelation for MaxEnt models

Authors: Varos Petrosyan, Fedor Osipov, Irina Feniova, Natalia Dergunova, Andrey Warshavsky, Lyudmila Khlyap, Andrew Dzialowski

Data type: figure (Pdf file)

Explanation note: Moran's I correlograms of residual spatial autocorrelation for MaxEnt models predicting the distribution of IAS in Russia and adjacent territories. These models were calibrated based on the SOR reported in the native and invasive range

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Link: https://doi.org/10.3897/neobiota.82.96282.suppl6

Supplementary material 7

The short description of invasive range of IAS in Russia

Authors: Varos Petrosyan, Fedor Osipov, Irina Feniova, Natalia Dergunova, Andrey Warshavsky, Lyudmila Khlyap, Andrew Dzialowski

Data type: table (xlsx file)

Explanation note: Short description of invasive range of IAS in Russia, current and potential types of distribution, and productive accuracy of MaxEnt SDMs (Bind±SE).

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Link: https://doi.org/10.3897/neobiota.82.96282.suppl7

Supplementary material 8

Species richness of IAS in Northern Eurasia

Authors: Varos Petrosyan, Fedor Osipov, Irina Feniova, Natalia Dergunova, Andrey Warshavsky, Lyudmila Khlyap, Andrew Dzialowski

Data type: table (xlsx file)

Explanation note: Species richness of terrestrial and aquatic IAS in the Russian regions and assessment of significance of hot and cold spots using Gi statistics.

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Link: https://doi.org/10.3897/neobiota.82.96282.suppl8